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THE SECOND CUSHING–HENSON CONJECTURE FOR THE BEVERTON–HOLT q-DIFFERENCE EQUATION

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Abstract. In this paper, we study the second Cushing–Henson conjecture for the Beverton–Holt difference equation with periodic inherent growth rate and periodic carrying capacity in the quantum calculus setting. We give a short summary of recent results regarding the Beverton–Holt difference and q-difference equation and introduce the theory of quantum calculus briefly. Next, we analyze the second Cushing–Henson conjecture. We extend recent studies in [*The Beverton-Holt q-difference equation with periodic growth rate*, Difference Equations, Discrete Dynamical Systems, and Applications, Springer-Verlag, Berlin, Heidelberg, New York, 2015, pp. 3–14] and state a modified formulation of the second Cushing–Henson conjecture for the Beverton–Holt q-difference equation as a generalization of existing formulations.

Keywords: Beverton–Holt equation, Cushing–Henson conjectures, q-difference equation, periodic solution.

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1. THE BEVERTON–HOLT DIFFERENCE EQUATION

Beverton and Holt introduced their population model in the context of fisheries in 1957 [3]. The model is applied in various fields such as biology, economy and social science, see [2, 15, 17]. To achieve a more realistic presentation of population dynamics, additional assumptions have been added to the traditional model such as contest competition [11], within-year resource limited competition [14], and including survivor rates [13].

The classical Beverton–Holt difference equation is given by

$$x_{n+1} = \frac{\nu K x_n}{K + (\nu - 1)x_n}, \quad n \in \mathbb{N}_0, \tag{1.1}$$

where $x_0 > 0$, $\nu > 1$ is the inherent growth rate, and $K > 0$ is representing the carrying capacity. Studies in [8] verify the first and the second Cushing–Henson conjecture for the classical Beverton–Holt equation. The first conjecture guarantees the existence of a unique periodic solution that is globally attractive. The second Cushing–Henson conjecture states that the average of the periodic solution is strictly less than the average of the periodic carrying capacity over one period. Biologically this means that the introduction of a periodic environment is deleterious for the population.

In [9], the periodically forced Beverton–Holt difference equation with periodic coefficients was introduced as

$$x_{n+1} = \frac{\nu_n K_n x_n}{K_n + (\nu_n - 1)x_n}, \quad n \in \mathbb{N}_0, \tag{1.2}$$

where $x_0 > 0$, $\nu_n > 1$ is the inherent growth rate, and K_n represents the positive periodic carrying capacity for all $n \in \mathbb{N}_0$. The following conjectures were confirmed.

Theorem 1.1 ([9, Conjecture 2.1]). *The difference equation* (1.2) *with ω-periodic K and ν has a unique ω-periodic solution that globally attracts all its solutions.*

Theorem 1.1 is a generalization of the first Cushing–Henson conjecture formulated for the classical Beverton–Holt equation with constant inherent growth rate. Cushing and Henson also predicted for the classical Beverton–Holt equation with constant growth rate that the introduction of a periodic environment is deleterious for the population [12]. However, in the case of a periodic growth rate, the authors provided a counterexample in [9] and presented the following modifications.

Theorem 1.2 ([9, Conjecture 3.2]). *The weighted average of the ω-periodic solution $\bar{x}$ of* (1.2) *is strictly less than the weighted average of the nonconstant ω-periodic carrying capacity K over one ω-period, i.e.,*

$$\frac{1}{a}\sum_{n=0}^{\omega-1} \alpha_n \bar{x}_n < \frac{1}{a}\sum_{n=0}^{\omega-1} \alpha_n K_n, \quad \text{where} \quad a = \sum_{n=0}^{\omega-1} \alpha_n, \tag{1.3}$$

with $\alpha = \frac{\nu-1}{\nu}$. If the carrying capacity K is constant, then we have equality in (1.3).

Theorem 1.3 ([9, Theorem 3.3]). *The average of the ω-periodic solution $\bar{x}$ of* (1.2) *is strictly less than the average of the "surrounded" nonconstant ω-periodic carrying capacity K, i.e.,*

$$\frac{1}{\omega}\sum_{n=0}^{\omega-1} \bar{x}_n < \frac{1}{\omega}\sum_{n=0}^{\omega-1} K_n(1+\delta_n) \tag{1.4}$$

with

$$\delta_n = \frac{\lambda+1}{\lambda}\sum_{i=1}^{\omega-1}(\alpha_n - \alpha_{n+i})\prod_{k=n+1}^{n+i-1}(1-\alpha_k).$$

If the carrying capacity K is constant, then we have equality in (1.4).

Theorems 1.2 and 1.3 clearly indicate that the classical second Cushing–Henson conjecture is only satisfied for special choices of periodic α.

In the following, we study the quantum calculus version of the Beverton–Holt equation, namely the Beverton–Holt q-difference equation. The equation was formulated and its unique one-periodic solution was derived in [5]. In [5], the authors also analyzed the Cushing–Henson conjectures for the case of a one-periodic inherent growth rate. A one-periodic inherent growth rate for the q-difference equation corresponds to a constant inherent growth rate in the classical Beverton–Holt model. Recently, the periodically forced Beverton–Holt q-difference equation with periodic coefficients has been studied in [10], and the Cushing–Henson conjectures were discussed. In this work, we extend the study of the Beverton–Holt q-difference equation with periodic growth rate and periodic carrying capacity and aim for a modification of the second Cushing–Henson conjecture consistent with the existing formulations. We begin the investigation with a brief introduction to quantum calculus.

2. SOME QUANTUM CALCULUS ESSENTIALS

In this section, we provide some quantum calculus prerequisites. Throughout, let $q > 1$.

Definition 2.1 ([6, Definition 1.1])**.** The forward jump operator $\sigma : q^{\mathbb{N}_0} \to q^{\mathbb{N}_0}$ is defined by

$$\sigma(t) := qt, \quad t \in q^{\mathbb{N}_0}.$$

Definition 2.2 ([6, Definition 2.25])**.** A function $p : q^{\mathbb{N}_0} \to \mathbb{R}$ is called regressive provided

$$1 + \mu(t)p(t) \neq 0 \quad \text{for all } t \in q^{\mathbb{N}_0}, \text{ where } \mu(t) = (q-1)t.$$

The set of all regressive functions is denoted by $\mathcal{R}$. Moreover, $p \in \mathcal{R}$ is called positively regressive, denoted by $p \in \mathcal{R}^+$, if

$$1 + \mu(t)p(t) > 0 \quad \text{for all } t \in q^{\mathbb{N}_0}.$$

Using the introduced "graininess" μ, the derivative can be defined as follows.

Definition 2.3. The derivative of a function $f : q^{\mathbb{N}_0} \to \mathbb{R}$ is given by

$$f^{\Delta}(t) = \frac{f(\sigma(t)) - f(t)}{\mu(t)} = \frac{f(qt) - f(t)}{(q-1)t} \quad \text{for all } t \in q^{\mathbb{N}_0}.$$

Theorem 2.4 ([6, Theorem 2.62])**.** *Suppose $p \in \mathcal{R}$. Let $t_0 \in q^{\mathbb{N}_0}$ and $y_0 \in \mathbb{R}$. The unique solution of the initial value problem*

$$y^{\Delta} = p(t)y, \quad y(t_0) = y_0$$

is given by

$$y = e_p(\cdot, t_0)y_0.$$

Theorem 2.5 ([6, Theorem 2.44])**.** *If $p \in \mathcal{R}^+$ and $t_0 \in q^{\mathbb{N}_0}$, then $e_p(t, t_0) > 0$ for all $t \in q^{\mathbb{N}_0}$.*

Definition 2.6 ([5])**.** Let $p \in \mathcal{R}$ and $s \in q^{\mathbb{N}_0}$. The exponential function is defined by

$$e_p(t,s) = \prod_{k \in [s,t) \cap q^{\mathbb{N}_0}} (1 + (q-1)kp(k)) \quad \text{for all } t \in q^{\mathbb{N}_0} \text{with } t > s,$$

$e_p(s,s) = 1$, and $e_p(t,s) = \frac{1}{e_p(s,t)}$ for $t < s$.

The integral in quantum calculus is defined in the following way.

Definition 2.7 ([5, Definition 2.6])**.** Let m, $n \in \mathbb{N}_0$ with $m < n$. For $f : q^{\mathbb{N}_0} \to \mathbb{R}$, we define

$$\int_{q^m}^{q^n} f(t)\,\Delta t := (q-1)\sum_{k=m}^{n-1} q^k f(q^k). \tag{2.1}$$

A special case follows directly by the previous definition.

$$\int_{q^m}^{q^{m+1}} f(t)\,\Delta t := (q-1)q^m f(q^m). \tag{2.2}$$

Theorem 2.8 ([6, Theorems 2.36 and 2.39])**.** *If $p \in \mathcal{R}$ and $a, b, c \in q^{\mathbb{N}_0}$, then*

$$\int_a^b p(t)e_p(t,c)\Delta t = e_p(b,c) - e_p(a,c), \tag{2.3}$$

$$\int_a^b p(t)e_p(c,\sigma(t))\Delta t = e_p(c,a) - e_p(c,b), \tag{2.4}$$

the semigroup property holds:

$$e_p(t,r)e_p(r,s) = e_p(t,s). \tag{2.5}$$

The following operations will be useful.

Definition 2.9 ([7, p. 10])**.** Define the "circle plus" addition on $\mathcal{R}$ as

$$(p \oplus q)(t) = p(t) + q(t) + (q-1)tp(t)q(t),$$

and the "circle minus" subtraction as

$$(p \ominus q)(t) = \frac{p(t) - q(t)}{1 + (q-1)tq(t)}.$$

Theorem 2.10 ([7, Theorem 1.39])**.** *Assume $p, q \in \mathcal{R}$. Then*

$$e_{p \oplus q}(t,s) = e_p(t,s)e_q(t,s), \tag{2.6}$$

$$e_{\ominus p}(t,s) = e_p(s,t) = \frac{1}{e_p(t,s)}. \tag{2.7}$$

Besides the circle plus and circle minus operation, a circle dot operation is defined as follows.

Definition 2.11 ([7, p. 18]). The circle dot multiplication $\odot$ of a constant $\alpha \in \mathbb{R}$ and a function $p \in \mathcal{R}^+$ is defined as

$$(\alpha \odot p)(t) = \alpha p(t) \int_0^1 (1 + \mu(t) h p(t))^{\alpha - 1} \mathrm{d}h.$$

Example 2.12. Let $p \in \mathcal{R}^+$ and $\alpha = \frac{1}{2}$. Then

$$\begin{aligned} \left(\frac{1}{2} \odot p\right)(t) &= \frac{1}{2} \int_0^1 \frac{p(t)}{\sqrt{1 + \mu(t) h p(t)}} \mathrm{d}h \\ &= \frac{1}{\mu(t)} \left(\sqrt{1 + \mu(t) p(t)} - 1\right) = \frac{p(t)}{1 + \sqrt{1 + \mu(t) p(t)}}. \end{aligned}$$

Note that by the definition of the circle dot multiplication,

$$\left(\frac{1}{2} \odot (-\alpha)\right) \oplus \left(\frac{1}{2} \odot (-\alpha)\right) = -\alpha.$$

We furthermore need the definition of periodicity for functions $f : q^{\mathbb{N}_0} \to \mathbb{R}$.

Definition 2.13 ([4, Definition 3.1]). A function $f : q^{\mathbb{N}_0} \to \mathbb{R}$ is called ω-periodic provided

$$f(t) = q^\omega f(q^\omega t) \text{ for all } t \in q^{\mathbb{N}_0}.$$

Lemma 2.14. *If $f, g \in \mathcal{R}$ are ω-periodic, then $f \oplus g$ and $f \ominus g$ is ω-periodic.*

Proof. We have

$$\begin{aligned} q^\omega (f \oplus g)(q^\omega t) &= q^\omega (f(q^\omega t) + g(q^\omega t) + \mu(q^\omega t) f(q^\omega t) g(q^\omega t)) \\ &= q^\omega (q^{-\omega} f(t) + q^{-\omega} g(t) + q^\omega \mu(t) q^{-\omega} f(t) q^{-\omega} g(t)) = (f \oplus g)(t) \end{aligned}$$

for all $t \in q^{\mathbb{N}_0}$, as well as

$$q^\omega (\ominus g)(q^\omega t) = q^\omega \frac{-g(q^\omega t)}{1 + \mu(q^\omega t) g(q^\omega t)} = q^\omega \frac{-q^{-\omega} g(t)}{1 + q^\omega \mu(t) q^{-\omega} g(t)} = (\ominus g)(t).$$

Using $f \ominus g = f \oplus (\ominus g)$ completes the proof. □

Lemma 2.15. *If $f \in \mathcal{R}$ is ω-periodic, then*

$$e_f(q^\omega t, q^\omega t_0) = e_f(t, t_0) \quad \textit{for all } t \in q^{\mathbb{N}_0} \tag{2.8}$$

and

$$e_f(q^\omega t, t) = e_f(q^\omega t_0, t_0) \quad \textit{for all } t \in q^{\mathbb{N}_0}. \tag{2.9}$$

Proof. Let $m, n \in \mathbb{N}_0$ such that $t_0 = q^m$ and $t = q^n$, and assume without loss of generality $t > t_0$. Then

$$\begin{aligned} e_f(q^\omega t, q^\omega t_0) &= \prod_{i=m+\omega}^{n+\omega-1} \big(1 + \mu(q^i) f(q^i)\big) \\ &= \prod_{i=m}^{n-1} \big(1 + \mu(q^{i+\omega}) f(q^{i+\omega})\big) = \prod_{i=m}^{n-1} \big(1 + q^\omega \mu(q^i) q^{-\omega} f(q^i)\big) \\ &= \prod_{i=m}^{n-1} \big(1 + \mu(q^i) f(q^i)\big) = e_f(t, t_0). \end{aligned}$$

For (2.9), note that

$$e_f(q^\omega t, t) = e_f(q^\omega t, q^\omega t_0) e_f(q^\omega t_0, t) = e_f(t, t_0) e_f(q^\omega t_0, t) = e_f(q^\omega t_0, t_0),$$

which completes the proof. □

3. THE BEVERTON–HOLT q-DIFFERENCE EQUATION

The Beverton–Holt q-difference equation was presented in [5] as

$$x(qt) = \frac{\nu(t) K(t) x(t)}{K(t) + (\nu(t) - 1) x(t)}, \tag{3.1}$$

where $K : q^{\mathbb{N}_0} \to \mathbb{R}^+$ is the carrying capacity, $\nu : q^{\mathbb{N}_0} \to (1, \infty)$ is the intrinsic growth rate, and $x : q^{\mathbb{N}_0} \to \mathbb{R}^+$ represents the population density. Using the substitution $a(t) = \frac{\nu(t)-1}{\mu(t)\nu(t)}$, we obtain the difference equation

$$x(qt) = \frac{K(t) x(t)}{(1 - \mu(t) a(t)) K(t) + \mu(t) a(t) x(t)}, \tag{3.2}$$

which is equivalent to

$$x(qt) K(t) - \mu(t) x(qt) a(t) K(t) + \mu(t) x(qt) a(t) x(t) = K(t) x(t),$$

i.e.,

$$x^\Delta(t) = x(qt) a(t) \left(1 - \frac{x(t)}{K(t)}\right). \tag{3.3}$$

Note that (3.3) is in the form of a logistic dynamic equation, introduced in [7]. This is considered to be the time scales analogue of the logistic differential equation

$$x'(t) = x(t) a(t) \left(1 - \frac{x(t)}{K(t)}\right).$$

The q-difference equation (3.3) is solved by using the transformation $u = 1/x$, which yields

$$u^{\Delta}(t) = -a(t)u(t) + \frac{a(t)}{K(t)}.$$

This is a first-order q-difference equation with the solution given in [6] as

$$u(t) = e_{-a}(t,t_0)u(t_0) + \int_{t_0}^{t} e_{-a}(t,qs)\frac{a(s)}{K(s)}\Delta s. \tag{3.4}$$

In [5], (3.1) was discussed considering a one-periodic growth rate ν. The authors provided the first Cushing–Henson conjecture and therefore the existence of a unique periodic solution that is globally attractive. In [10], the authors generalized the discussion to the Beverton–Holt q-difference equation with periodic coefficients and obtained the following conjecture.

Theorem 3.1 (First Cushing–Henson Conjecture)**.** *Assume*

$$\begin{cases} K : q^{\mathbb{N}_0} \to \mathbb{R}^+ & \text{is } \omega\text{-periodic}, \\ a : q^{\mathbb{N}_0} \to \mathbb{R}^+ & \text{is } \omega\text{-periodic and } -a \in \mathcal{R}^+, \\ e_{-a}(t_0q^{\omega}, t_0) \neq q^{\omega}. \end{cases} \tag{3.5}$$

Then (3.2) *has a unique ω-periodic solution that globally attracts all its solutions.*

The unique ω-periodic solution is given in [10] as

$$\bar{x}(t) = \lambda \left(\int_{t}^{tq^{\omega}} e_{-a}(t,\sigma(s))\frac{a(s)}{K(s)}\Delta s \right)^{-1}, \tag{3.6}$$

where

$$\lambda = q^{\omega}e_{-a}(t_0, t_0q^{\omega}) - 1 \neq 0.$$

Cushing and Henson predicted further that the introduction of a periodic environment is deleterious to the population, i.e, the average of the periodic solution is strictly less than the average of the carrying capacity. The authors in [5] investigated the Beverton–Holt q-difference equation with one-periodic inherent growth rate. Already in the case of a one-periodic growth rate ν, the second Cushing–Henson conjecture was not satisfied and the authors offered the following modification.

Theorem 3.2 ([5, Theorem 5.6])**.** *If a is one-periodic, i.e., $a(t) = \frac{\alpha}{t}$, $\alpha \in \mathbb{R}^+$, and K is ω-periodic, then the average of the unique ω-periodic solution is strictly less than the average of the carrying capacity times a constant, i.e.,*

$$\frac{1}{\omega}\int_{t_0}^{t_0q^{\omega}} \bar{x}(t)\,\Delta t < \frac{\alpha+1}{\alpha}\left\{ \frac{1}{\omega}\int_{t_0}^{t_0q^{\omega}} K(t)\,\Delta t \right\}. \tag{3.7}$$

If K is one-periodic, then (3.7) *becomes an equality.*

Note that a one-periodic function is a constant function in the discrete and continuous time setting. The analysis of the Beverton–Holt q-difference equation was extended to an ω-periodic growth rate in [10] and the following results were obtained.

Theorem 3.3 ([10, Conjecture 2])**.** *The average of the ω-periodic solution $\bar{x}$ of* (3.2) *is strictly less than the average of the ω-periodic carrying capacity K times a function v over one ω-period, where $v(t) = C(r(t) - 1)$ with*

$$C = \frac{\lambda}{(e_{-a}(t_0, t_0 q^\omega) - 1)^2} \frac{q}{(q-1)} \frac{1}{t_0 q^\omega}$$

and

$$r(t) = 2\frac{1 - \sqrt{1 - \mu(t)a(t)}}{\mu(t)a(t)},$$

i.e.,

$$\frac{1}{\omega(q-1)} \int_{t_0}^{t_0 q^\omega} \bar{x}(t)\Delta t < \frac{1}{\omega(q-1)} \int_{t_0}^{t_0 q^\omega} v(t)K(t)\Delta t,$$

with equality for K constant.

Note that the last two conjectures are equalities if the carrying capacity is constant. In this paper, we relate the periodic solution and the periodically forced environment in such a way that the upper bound is obtained for an element of the family of periodic environments. This differs from the obtained results as a constant function is not (one-)periodic by Definition 2.13.

We also need to define the average of a function in the quantum calculus setting. To do so, let us recall the construction of the average of a function in the continuous and discrete cases. For $f \in \mathcal{C}(\mathbb{R})$, the average of a function on $[a, b]$ is defined as:

$$f_{\text{av}} = \frac{1}{b-a} \int_a^b f(t)\mathrm{d}t$$

and in the discrete case

$$f_{\text{av}} = \frac{1}{n} \sum_{i=0}^{n-1} f(i).$$

In particular, if $f(t) = F$, F constant, then $f_{\text{av}} = F$ in the continuous and the discrete time setting. The reason is that we essentially take the average value of the area under the function. A constant function in the discrete and continuous setting corresponds to a one-periodic function in the quantum calculus setting; so we consider $f : q^{\mathbb{N}_0} \to \mathbb{R}$, $f(t) = \frac{F}{t}$. Similar as in the discrete case, the integral expression represents the area of rectangles, see (2.1). To understand the normalization factor C such that $f_{av} = \frac{1}{C} \int_a^b f(s)\Delta s$, let us realize that the area of the rectangles is constant for each rectangle, i.e., $f(t)d(t, qt) = f(s)d(s, qs)$, see Figure 1.

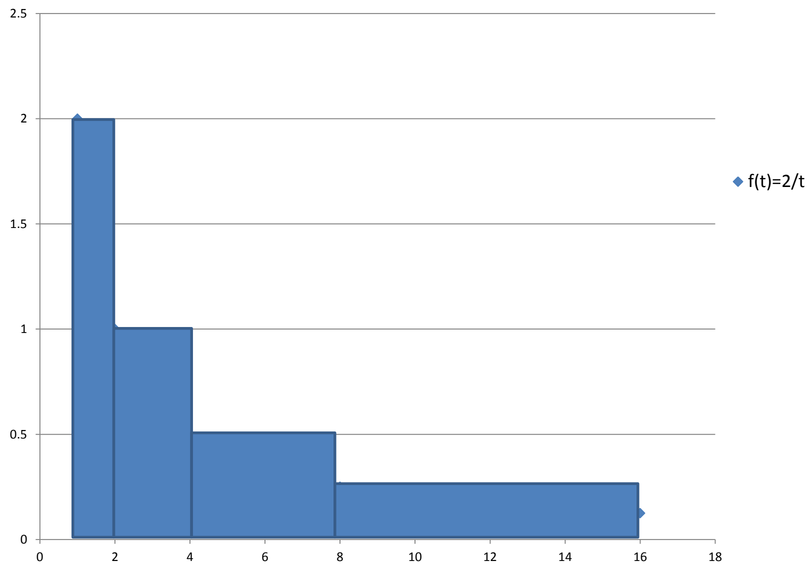

Fig. 1. An example of a one-periodic function $f(t) = \frac{2}{t}$ for $2^{\mathbb{N}_0}$

Since the area of the rectangles is preserved, every rectangle has an area of $f(q^0)\mu(q^0) = F(q-1)$. If we add all n rectangles, we obtain $F(q-1)n$ as the total area. We therefore have

$$F = f_{\text{av}} = \frac{1}{C}\int_{t_0}^{q^\omega t_0} f(s)\Delta s = \frac{1}{C}\sum_{i=0}^{\omega-1}\mu(q^i)\frac{F}{q^i} = \frac{1}{C}F(q-1)\omega.$$

This gives the normalization constant as $C = \omega(q-1)$. Note that we can always reduce the area of such a rectangle to the area formed by $f(q^0)(q-1)$, even if the lower boundary is not q^0. We therefore formulate the average of a function $f : q^{\mathbb{N}_0}$ in the following way.

Definition 3.4. The average of a function $f : q^{\mathbb{N}_0} \to \mathbb{R}$ on the interval $[t, q^\omega t] \cap q^{\mathbb{N}_0}$ is

$$f_{\text{av}} = \frac{1}{\omega(q-1)}\int_{t}^{q^\omega t} f(s)\Delta s.$$

Using the definition of averages in the quantum calculus setting, we can now formulate theorems relating averages of the periodic solution to the periodic carrying capacity. Let us initiate the discussion by investigating the Beverton–Holt q-difference equation with a two-periodic growth rate.

4. TWO-PERIODIC GROWTH RATE

Let us first define the minimal periodicity of a function.

Definition 4.1. A function $p : q^{\mathbb{N}_0} \to \mathbb{R}$ is said to be periodic with order ω or order ω-periodic, if $\omega \in \mathbb{N}$ is the smallest possible value such that $q^\omega p(q^\omega t) = p(t)$ for all $t \in q^{\mathbb{N}_0}$.

Lemma 4.2. *If $p : q^{\mathbb{N}_0} \to \mathbb{R}$ is periodic with order ω, then there exist constants $p_0, p_1, \dots, p_{\omega-1}$ such that*

$$p(t) = \frac{p_i}{t}, \qquad \textit{where } i = (\log_q t) \ (\textit{mod } \omega). \tag{4.1}$$

Proof. If p is any order ω-periodic function, then $tp(t)$ can take at most ω different values, namely $p_i := q^i t_0 p(q^i t_0)$. To realize that, let $t \in q^{\mathbb{N}_0}$. Then there exist $n, m \in \mathbb{N}_0$, such that $t = q^{n\omega+m}$, where $0 \le m \le \omega - 1$. We have

$$tp(t) = q^{n\omega+m} p(q^{n\omega+m}) = q^{n\omega} q^m p(q^{n\omega} q^m) = q^m p(q^m) = p_m,$$

where $0 \le m \le \omega - 1$. This completes the proof. □

Note that

$$\log_q(tq^\omega) \ (\text{mod } \omega) = (\log_q t) \ (\text{mod } \omega) + \omega \ (\text{mod } \omega) = \log_q t \ (\text{mod } \omega).$$

In the special case of an order two-periodic function $p : q^{\mathbb{N}_0} \to \mathbb{R}$, we have

$$p(t) = \begin{cases} \frac{\rho_0}{t} & \text{if } \log_q t \text{ is even,} \\ \frac{\rho_1}{t} & \text{if } \log_q t \text{ is odd} \end{cases} \tag{4.2}$$

for ρ_i constant, $i = 0, 1$, and $\rho_0 \neq \rho_1$.

Theorem 4.3. *The average of the two-periodic solution $\bar{x}$ of* (3.2) *is strictly less than the average of $\lambda v K/(q-1)$, i.e.,*

$$\frac{1}{2(q-1)} \int_{t_0}^{t_0 q^2} \bar{x}(t) \Delta t < \frac{\lambda}{2(q-1)^2} \int_{t_0}^{t_0 q^2} v(t) K(t) \Delta t, \tag{4.3}$$

where

$$\lambda = q^2 e_{-a}(t_0, t_0 q^2) - 1,$$

and

$$v(t) = \frac{A_{\log_q t}}{\left(A_{\log_q t} + q B_{\log_q t}\right)^2} + q \frac{B_{\log_q (t+1)}}{\left(A_{\log_q (t+1)} + q B_{\log_q (t+1)}\right)^2}$$

with $A_n := \frac{a_n}{1-(q-1)a_n}$ and $B_n := \frac{A_n A_{n+1}}{a_n}$, $n = 0, 1$, and $\log_q t = \log_q t$ (mod 2). If K is one-periodic, then (4.3) *becomes an equality.*

Useful in the proof of Theorem 4.3 is the following lemma.

Lemma 4.4. *Let* $f : q^{\mathbb{N}_0} \times q^{\mathbb{N}_0} \to \mathbb{R}$, $\omega \in \mathbb{N}_0$. *Then*

$$\int_{t_0}^{t_0 q^\omega} \int_{t}^{t q^\omega} f(s,t)\Delta s\,\Delta t = \int_{t_0}^{t_0 q^\omega} \int_{t_0}^{sq} f(s,t)\Delta t\,\Delta s + \int_{t_0 q^\omega}^{t_0 q^{2\omega}} \int_{sq^{1-\omega}}^{t_0 q^\omega} f(s,t)\Delta t\,\Delta s. \tag{4.4}$$

Proof. Let $t_0 = q^m$, $m \in \mathbb{N}_0$. Then

$$\begin{aligned}
\int_{t_0}^{t_0 q^\omega} \int_{t}^{t q^\omega} f(s,t)\Delta s\,\Delta t &\overset{(2.1)}{=} (q-1)\sum_{k=m}^{m+\omega-1} q^k (q-1) \sum_{i=k}^{k+\omega-1} q^i f(q^i, q^k) \\
&= (q-1)\sum_{i=m}^{m+\omega-1} q^i (q-1) \sum_{k=m}^{i} q^k f(q^i, q^k) \\
&\quad + (q-1)\sum_{i=m+\omega}^{m+2\omega-2} q^i (q-1) \sum_{k=i+1-\omega}^{m+\omega-1} q^k f(q^i, q^k) \\
&\overset{(2.1)}{=} \int_{t_0}^{t_0 q^\omega} \int_{t_0}^{sq} f(s,t)\Delta t\,\Delta s + \int_{t_0 q^\omega}^{t_0 q^{2\omega}} \int_{sq^{1-\omega}}^{t_0 q^\omega} f(s,t)\Delta t\,\Delta s \\
&\quad - \int_{t_0 q^{2\omega-1}}^{t_0 q^{2\omega}} \int_{sq^{1-\omega}}^{t_0 q^\omega} f(s,t)\Delta t\,\Delta s \\
&= \int_{t_0}^{t_0 q^\omega} \int_{t_0}^{sq} f(s,t)\Delta t\,\Delta s + \int_{t_0 q^\omega}^{t_0 q^{2\omega}} \int_{sq^{1-\omega}}^{t_0 q^\omega} f(s,t)\Delta t\,\Delta s,
\end{aligned}$$

where we have used that $\int_c^c f(s)\Delta s = 0$. This completes the proof. □

Proof of Theorem 4.3. Let $t_0 = q^m$, $m \in \mathbb{N}_0$. Since a and K are two-periodic, $a(t) = \frac{\alpha_t}{t}$ and $K(t) = \frac{\kappa_t}{t}$ as in (4.2). Applying the weighted Jensen inequality [18, Theorem 2.2] (see also [1]), we get

$$\int_{t_0}^{t_0q^2} \bar{x}(t)\Delta t \overset{(3.6)}{=} \int_{t_0}^{t_0q^2} \frac{\lambda}{\int_t^{tq^2} e_{-a}(t,\sigma(s))\frac{a(s)}{K(s)}\Delta s}\Delta t$$

$$= \int_{t_0}^{t_0q^2} \frac{\lambda}{\int_t^{tq^2} e_{-a}(t,\sigma(s))\frac{a(s)s}{K(s)s}\Delta s}\Delta t$$

$$< \lambda \int_{t_0}^{t_0q^2} \frac{\int_t^{tq^2} e_{-a}(t,\sigma(s))a(s)K(s)s^2\Delta s}{\left(\int_t^{tq^2} e_{-a}(t,\sigma(s))a(s)s\Delta s\right)^2}\Delta t$$

$$= \lambda \int_{t_0}^{t_0q^2} \frac{\int_t^{tq^2} e_{-a}(t,\sigma(s))\alpha_s\kappa_s\Delta s}{\left(\int_t^{\sigma(t)} e_{-a}(t,\sigma(s))\alpha_s\Delta s + \int_{tq}^{\sigma(tq)} e_{-a}(t,\sigma(s))\alpha_s\Delta s\right)^2}\Delta t$$

$$\overset{(2.1)}{=} \lambda \int_{t_0}^{t_0q^2} \frac{\int_t^{tq^2} e_{-a}(t,\sigma(s))\alpha_s\kappa_s\Delta s}{\left[\mu(t)e_{-a}(t,tq)\alpha_t + \mu(qt)e_{-a}(t,tq^2)\alpha_{tq}\right]^2}\Delta t$$

$$= \lambda \int_{t_0}^{t_0q^2}\int_t^{tq^2} \frac{1}{\mu^2(t)} \frac{e_{-a}(t,\sigma(s))\alpha_s\kappa_s}{\left[e_{-a}(t,tq)\alpha_t + qe_{-a}(t,tq^2)\alpha_{tq}\right]^2}\Delta s\,\Delta t$$

$$\overset{(4.4)}{=} \lambda \int_{t_0}^{t_0q^2}\int_{t_0}^{sq} \frac{1}{\mu^2(t)} \frac{e_{-a}(t,\sigma(s))\alpha_s\kappa_s}{\left[e_{-a}(t,tq)\alpha_t + qe_{-a}(t,tq^2)\alpha_{tq}\right]^2}\Delta t\,\Delta s$$

$$+ \lambda \int_{t_0q^2}^{t_0q^4}\int_{sq^{-1}}^{t_0q^2} \frac{1}{\mu^2(t)} \frac{e_{-a}(t,\sigma(s))\alpha_s\kappa_s}{\left[e_{-a}(t,tq)\alpha_t + qe_{-a}(t,tq^2)\alpha_{tq}\right]^2}\Delta t\,\Delta s.$$

Denote $\alpha_{t_0} = \alpha_0$, $\alpha_{qt_0} = \alpha_1$, $\kappa_{t_0} = \kappa_0$, and $\kappa_{qt_0} = \kappa_1$. By integrating, the last expression is equal to

$$\begin{aligned}
&\lambda\mu(t_0)\int_{t_0}^{t_0 q}\frac{1}{\mu^2(t)}\frac{e_{-a}(t,t_0q)\alpha_0\kappa_0}{\left[e_{-a}(t,tq)\alpha_t+qe_{-a}(t,tq^2)\alpha_{tq}\right]^2}\Delta t\\
&\quad+\lambda\mu(qt_0)\int_{t_0}^{t_0 q}\frac{1}{\mu^2(t)}\frac{e_{-a}(t,t_0q^2)\alpha_1\kappa_1}{\left[e_{-a}(t,tq)\alpha_t+qe_{-a}(t,tq^2)\alpha_{tq}\right]^2}\Delta t\\
&\quad+\lambda\mu(qt_0)\int_{t_0 q}^{t_0 q^2}\frac{1}{\mu^2(t)}\frac{e_{-a}(t,t_0q^2)\alpha_1\kappa_1}{\left[e_{-a}(t,tq)\alpha_t+qe_{-a}(t,tq^2)\alpha_{tq}\right]^2}\Delta t\\
&\quad+\lambda\mu(q^2t)\int_{t_0 q}^{t_0 q^2}\frac{1}{\mu^2(t)}\frac{e_{-a}(t,t_0q^3)\alpha_0\kappa_0}{\left[e_{-a}(t,tq)\alpha_t+qe_{-a}(t,tq^2)\alpha_{tq}\right]^2}\Delta t\\
&\overset{(2.1)}{=}\lambda\frac{e_{-a}(t_0,t_0q)\kappa_0\alpha_0}{\left[e_{-a}(t_0,t_0q)\alpha_0+qe_{-a}(t_0,t_0q^2)\alpha_1\right]^2}\\
&\quad+\lambda q\frac{e_{-a}(t_0,t_0q^2)\kappa_1\alpha_1}{\left[e_{-a}(t_0,t_0q)\alpha_0+qe_{-a}(t_0,t_0q^2)\alpha_1\right]^2}\\
&\quad+\lambda\frac{e_{-a}(t_0q,t_0q^2)\kappa_1\alpha_1}{\left[e_{-a}(t_0q,t_0q^2)\alpha_1+qe_{-a}(t_0q,t_0q^3)\alpha_0\right]^2}\\
&\quad+\lambda q\frac{e_{-a}(t_0q,t_0q^3)\kappa_0\alpha_0}{\left[e_{-a}(t_0q,t_0q^2)\alpha_1+qe_{-a}(t_0q,t_0q^3)\alpha_0\right]^2},
\end{aligned}$$

where we have applied the periodicity condition on a and K. Using the definition of the exponential function, the last expression is equal to

$$\begin{aligned}
&\lambda\frac{\frac{1}{1-(q-1)\alpha_0}}{\left(\frac{\alpha_0}{1-(q-1)\alpha_0}+q\frac{\alpha_1}{(1-(q-1)\alpha_0)(1-(q-1)\alpha_1)}\right)^2}\kappa_0\alpha_0\\
&\quad+\lambda q\frac{\frac{1}{(1-(q-1)\alpha_0)(1-(q-1)\alpha_1)}}{\left(\frac{\alpha_0}{1-(q-1)\alpha_0}+q\frac{\alpha_1}{(1-(q-1)\alpha_0)(1-(q-1)\alpha_1)}\right)^2}\kappa_1\alpha_1\\
&\quad+\lambda\frac{\frac{1}{1-(q-1)\alpha_1}}{\left(\frac{\alpha_1}{1-(q-1)\alpha_1}+q\frac{\alpha_0}{(1-(q-1)\alpha_0)(1-(q-1)\alpha_1)}\right)^2}\kappa_1\alpha_1\\
&\quad+\lambda q\frac{\frac{1}{(1-(q-1)\alpha_0)(1-(q-1)\alpha_1)}}{\left(\frac{\alpha_1}{1-(q-1)\alpha_1}+q\frac{\alpha_0}{(1-(q-1)\alpha_0)(1-(q-1)\alpha_1)}\right)^2}\kappa_0\alpha_0.
\end{aligned}$$

Introducing $A_n := \frac{\alpha_n}{1-(q-1)\alpha_n}$ and rearranging terms, we can express the previous expression as

$$\lambda\kappa_0\left(\frac{A_0}{\left(A_0+qA_1\frac{1}{1-(q-1)\alpha_0}\right)^2}+q\frac{A_0\frac{1}{1-(q-1)\alpha_1}}{\left(A_1+qA_0\frac{1}{1-(q-1)\alpha_1}\right)^2}\right)$$
$$+\lambda\kappa_1\left(\frac{A_1}{\left(A_1+qA_0\frac{1}{1-(q-1)\alpha_1}\right)^2}+q\frac{A_1\frac{1}{1-(q-1)\alpha_0}}{\left(A_0+qA_1\frac{1}{1-(q-1)\alpha_0}\right)^2}\right).$$

Introducing the notation $B_n := \frac{A_{n-1}A_n}{\alpha_n}$ yields the result. The weighted Jensen inequality is an equality if the nonweight is constant w.r.t. the integrating variable [16, p. 298]. In our case, the condition translates to $K(s)s = \kappa$, i.e., $K(s) = \frac{\kappa}{s}$ for $\kappa \in \mathbb{R}$. Hence K is one-periodic. □

Remark 4.5. If a is one-periodic, then $a(t) = \frac{\alpha}{t}$, i.e., $\alpha_0 = \alpha_1 = \alpha$ for $0 < (q-1)\alpha < 1$. We then have

$$\begin{aligned}
v(t) &= \left(\frac{A}{\left(A+q\frac{A^2}{\alpha}\right)^2}+q\frac{\frac{A^2}{\alpha}}{\left(A+q\frac{A^2}{\alpha}\right)^2}\right)\\
&= \frac{\frac{\alpha}{1-(q-1)\alpha}}{\left(\frac{\alpha}{1-(q-1)\alpha}+q\frac{\alpha}{(1-(q-1)\alpha)^2}\right)^2}+q\frac{\frac{\alpha}{(1-(q-1)\alpha)^2}}{\left(\frac{\alpha}{1-(q-1)\alpha}+q\frac{\alpha}{(1-(q-1)\alpha)^2}\right)^2}\\
&= \frac{1}{\frac{\alpha}{1-(q-1)\alpha}\left(1+q\frac{1}{(1-(q-1)\alpha)}\right)^2}+q\frac{1}{\alpha\left(1+q\frac{1}{(1-(q-1)\alpha)}\right)^2}\\
&= \frac{1}{\left(1+q\frac{1}{(1-(q-1)\alpha)}\right)^2}\left(\frac{1-(q-1)\alpha+q}{\alpha}\right) = \frac{(1-(q-1)\alpha)^2}{(1+q-(q-1)\alpha)}\frac{1}{\alpha}.
\end{aligned}$$

That yields

$$\lambda v(t) = \left(\frac{q^2}{(1-(q-1)\alpha)^2}-1\right)\frac{(1-(q-1)\alpha)^2}{(1+q-(q-1)\alpha)}\frac{1}{\alpha} = (q-1)\frac{1+\alpha}{\alpha}.$$

Theorem 4.3 reads now as

$$\frac{1}{2(q-1)}\int_{t_0}^{t_0q^2}\bar{x}(t)\Delta t < \frac{1}{2(q-1)}\frac{1+\alpha}{\alpha}\int_{t_0}^{t_0q^2}K(t)\Delta t,$$

which is consistent with (3.7).

Example 4.6. Let us consider the following example, where a, K are 2-periodic with the values

$$a(q^n) = \begin{cases}\frac{0.2}{q^n} & \text{if } n \text{ is even,}\\ \frac{0.5}{q^n} & \text{if } n \text{ is odd,}\end{cases} \qquad K(q^n) = \begin{cases}\frac{0.6}{q^n} & \text{if } n \text{ is even,}\\ \frac{0.8}{q^n} & \text{if } n \text{ is odd,}\end{cases} \tag{4.5}$$

$n \in \mathbb{N}_0$ and $t_0 = q = 1.2$. The inequality provided in Theorem 4.3 is visualized in Figure 2.

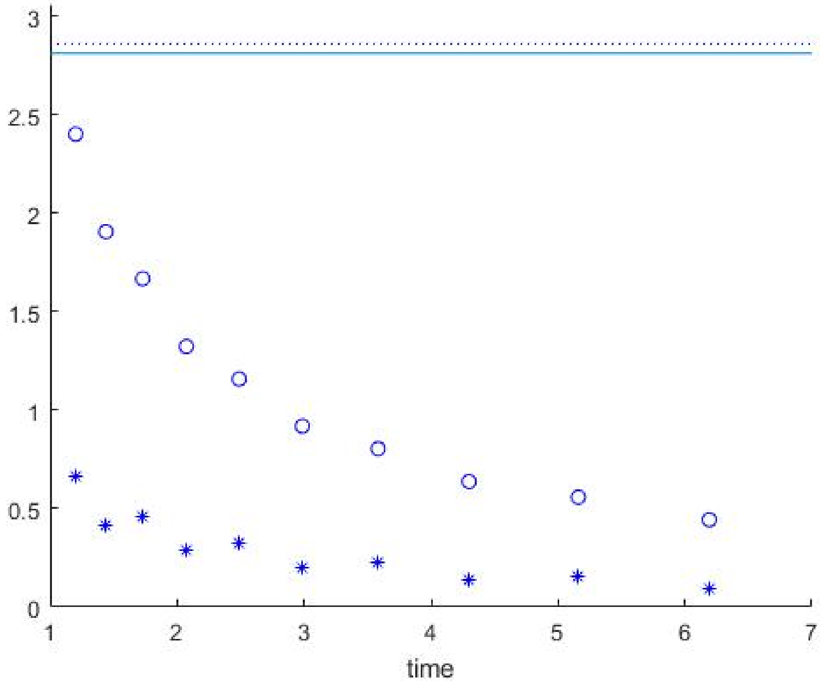

Fig. 2. Carrying capacity given by $*$, solution by o. Solid line is the average of the 2-periodic solution, dashed line is the average of the weighted carrying capacity.

Example 4.7. Let us slightly change the carrying capacity from Example 4.6 and consider the 2-periodic coefficients

$$a(q^n) = \begin{cases} \frac{0.2}{q^n} & \text{if } n \text{ is even,} \\ \frac{0.5}{q^n} & \text{if } n \text{ is odd,} \end{cases} \qquad K(q^n) = \begin{cases} \frac{0.3}{q^n} & \text{if } n \text{ is even,} \\ \frac{0.9}{q^n} & \text{if } n \text{ is odd,} \end{cases} \tag{4.6}$$

and $t_0 = q = 1.2$. The inequality provided in Theorem 4.3 is visualized in Figure 3.

Recall that in the case of a 1-periodic carrying capacity, the average of the periodic solution is equal to the weighted average of the carrying capacity. In Figure 2, the 2-periodic factors of the carrying capacity are relatively close with 0.6 and 0.8. If the difference is however increased, assuming all other values fixed, we see that the difference between the average of the corresponding periodic solution and the weighted average of the carrying capacity is also increased, see Figure 3.

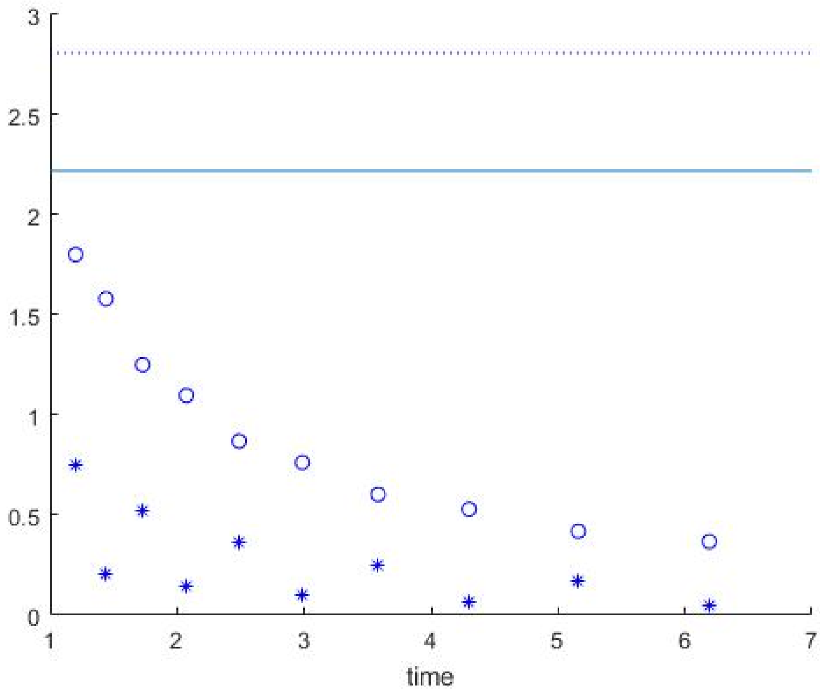

Fig. 3. Carrying capacity given by $*$, solution by o. Solid line is the average of the 2-periodic solution, dashed line is the average of the weighted carrying capacity.

5. ω-PERIODIC GROWTH RATE

Throughout this section, we assume (3.5). We present two inequalities relating the ω-periodic solution $\bar{x}$ and the ω-periodic environment. The first formulation is a generalization of the theorem we have discussed in the previous subsection for two-periodic coefficients.

Theorem 5.1. *The average of the ω-periodic solution $\bar{x}$ of* (3.2) *is strictly less than the average of the order ω-periodic carrying capacity K times a function, i.e.,*

$$\frac{1}{\omega(q-1)} \int_{t_0}^{t_0 q^\omega} \bar{x}(t)\Delta t < \frac{\lambda}{\omega(q-1)} \int_{t_0}^{t_0 q^\omega} v(t)K(t)\Delta t, \tag{5.1}$$

where $\lambda = q^\omega e_{-a}(t_0, q^\omega t_0) - 1$ and

$$v(s) = a(s)s^2 \left\{ \int_{t_0}^{\sigma(s)} \frac{e_{-a}(t,\sigma(s))}{\mu^2(t)g^2(t)}\Delta t + (\lambda+1) \int_{\sigma(s)}^{t_0 q^\omega} \frac{e_{-a}(t,\sigma(s))}{\mu^2(t)g^2(t)}\Delta t \right\},$$

with

$$g(t) := \sum_{n=0}^{\omega-1} q^n e_{-a}(t, tq^{n+1}) a(tq^n) tq^n.$$

The inequality (5.1) *is an equality if* K *is one-periodic.*

Proof. Let $t_0 = q^m$, $m \in \mathbb{N}_0$. Applying the weighted Jensen inequality [18, Theorem 2.2] yields

$$\begin{aligned}
\int_{t_0}^{t_0 q^\omega} \bar{x}(t)\Delta t &\overset{(3.6)}{=} \lambda \int_{t_0}^{t_0 q^\omega} \frac{1}{\int_t^{tq^\omega} e_{-a}(t,\sigma(s)) \frac{a(s)}{K(s)} \Delta s} \Delta t \\
&< \lambda \int_{t_0}^{t_0 q^\omega} \frac{\int_t^{tq^\omega} e_{-a}(t,\sigma(s)) a(s) K(s) s^2 \Delta s}{\left(\int_t^{tq^\omega} e_{-a}(t,\sigma(s)) a(s) s \Delta s \right)^2} \Delta t \\
&= \lambda \int_{t_0}^{t_0 q^\omega} \frac{\int_t^{tq^\omega} e_{-a}(t,\sigma(s)) a(s) K(s) s^2 \Delta s}{\left(\sum_{n=0}^{\omega-1} \int_{tq^n}^{\sigma(tq^n)} e_{-a}(t,\sigma(s)) a(s) s \Delta s \right)^2} \Delta t \\
&\overset{(2.2)}{=} \lambda \int_{t_0}^{t_0 q^\omega} \frac{\int_t^{tq^\omega} e_{-a}(t,\sigma(s)) a(s) K(s) s^2 \Delta s}{\left(\sum_{n=0}^{\omega-1} \mu(tq^n) e_{-a}(t,\sigma(tq^n)) a(tq^n) tq^n \right)^2} \Delta t \\
&= \lambda \int_{t_0}^{t_0 q^\omega} \frac{\int_t^{tq^\omega} e_{-a}(t,\sigma(s)) a(s) K(s) s^2 \Delta s}{\mu(t)^2 \left(\sum_{n=0}^{\omega-1} q^n e_{-a}(t, tq^{n+1}) a(tq^n) tq^n \right)^2} \Delta t.
\end{aligned}$$

Define

$$g(t) := \sum_{n=0}^{\omega-1} q^n e_{-a}(t, tq^{n+1}) a(tq^n) tq^n.$$

Then

$$g(q^\omega t) = \sum_{n=0}^{\omega-1} q^n e_{-a}(tq^\omega, tq^\omega q^{n+1}) a(tq^\omega q^n) tq^\omega q^n = \sum_{n=0}^{\omega-1} q^n e_{-a}(t, tq^{n+1}) a(tq^n) tq^n = g(t),$$

i.e., g takes at most ω different values. We therefore have

$$\begin{aligned}\int_{t_0}^{t_0 q^\omega} \bar{x}(t)\Delta t &< \lambda \int_{t_0}^{t_0 q^\omega} \int_{t}^{tq^\omega} \frac{e_{-a}(t,\sigma(s))a(s)K(s)s^2}{\mu(t)^2 g^2(t)} \Delta s\, \Delta t \\ &\overset{(4.4)}{=} \lambda \int_{t_0}^{t_0 q^\omega} a(s)K(s)s^2 \int_{t_0}^{sq} \frac{e_{-a}(t,\sigma(s))}{\mu(t)^2 g^2(t)} \Delta t\, \Delta s \\ &\quad + \lambda \int_{t_0 q^\omega}^{t_0 q^{2\omega}} a(s)K(s)s^2 \int_{sq^{1-\omega}}^{t_0 q^\omega} \frac{e_{-a}(t,\sigma(s))}{\mu(t)^2 g^2(t)} \Delta t\, \Delta s.\end{aligned}$$

Realize that we can write the second integral as

$$\begin{aligned}&\int_{t_0 q^\omega}^{t_0 q^{2\omega}} a(s)K(s)s^2 \int_{sq^{1-\omega}}^{t_0 q^\omega} \frac{e_{-a}(t,\sigma(s))}{\mu(t)^2 g^2(t)} \Delta t\, \Delta s \\ &\overset{(2.1)}{=} \sum_{l=m+\omega}^{m+2\omega-1} \mu(q^l)a(q^l)K(q^l)q^{2l} \sum_{k=l+1-\omega}^{m+\omega-1} \mu(q^k) \frac{e_{-a}(q^k,\sigma(q^l))}{\mu(q^k)^2 g^2(q^k)} \\ &= \sum_{l=m}^{m+\omega-1} \mu(q^{l+\omega})a(q^{l+\omega})K(q^{l+\omega})q^{2(l+\omega)} \sum_{k=l+1}^{m+\omega-1} \frac{e_{-a}(q^k,\sigma(q^{l+\omega}))}{\mu(q^k)g^2(q^k)} \\ &= \sum_{l=m}^{m+\omega-1} \mu(q^l)a(q^l)K(q^l)q^{2l}q^\omega \sum_{k=l+1}^{m+\omega-1} \frac{e_{-a}(t_0,t_0q^\omega)e_{-a}(q^k,\sigma(q^l))}{\mu(q^k)g^2(q^k)} \\ &\overset{(2.1)}{=} \int_{t_0}^{t_0 q^\omega} a(s)K(s)s^2 \int_{\sigma(s)}^{t_0 q^\omega} q^\omega e_{-a}(t_0,t_0q^\omega) \frac{e_{-a}(t,\sigma(s))}{\mu(t)^2 g^2(t)} \Delta t\, \Delta s \\ &= \int_{t_0}^{t_0 q^\omega} a(s)K(s)s^2 \int_{\sigma(s)}^{t_0 q^\omega} (\lambda+1) \frac{e_{-a}(t,\sigma(s))}{\mu(t)^2 g^2(t)} \Delta t\, \Delta s.\end{aligned}$$

We can write the obtained upper bound now as

$$\lambda \int_{t_0}^{t_0 q^\omega} a(s)K(s)s^2 \left\{ \int_{t_0}^{\sigma(s)} \frac{e_{-a}(t,\sigma(s))}{\mu(t)^2 g^2(t)} \Delta t \, + (\lambda+1) \int_{\sigma(s)}^{t_0 q^\omega} \frac{e_{-a}(t,\sigma(s))}{\mu(t)^2 g^2(t)} \Delta t \right\} \Delta s.$$

If K is one-periodic, then the weighted Jensen inequality yields equality [16, p. 298]. □

Note that the function v does not depend on the choice of K, only on a. By using the special structure of periodic functions suggested in (4.1), $a(t) = \frac{a_t}{t}$ and $K(t) = \frac{K_t}{t}$, the inequality (5.1) reads as

$$\begin{aligned} &\frac{1}{\omega(q-1)} \int_{t_0}^{t_0 q^\omega} \bar{x}(t) \Delta t \\ &< \frac{\lambda}{\omega(q-1)} \int_{t_0}^{t_0 q^\omega} K_s a_s \left\{ \int_{t_0}^{\sigma(s)} \frac{e_{-a}(t,\sigma(s))}{\mu(t)^2 g^2(t)} \Delta t + (\lambda+1) \int_{\sigma(s)}^{t_0 q^\omega} \frac{e_{-a}(t,\sigma(s))}{\mu(t)^2 g^2(t)} \Delta t \right\} \Delta s, \end{aligned}$$

where

$$g(t) = \sum_{n=0}^{\omega-1} q^n e_{-a}(t, tq^{n+1}) a_{tq^n}.$$

A slightly different expression of (5.1) is possible:

$$\begin{aligned} &\frac{1}{\omega(q-1)} \int_{t_0}^{t_0 q^\omega} \bar{x}(t) \Delta t \\ &< \frac{\lambda}{\omega(q-1)} \int_{t_0}^{t_0 q^\omega} K(s)a(s)s^2 \left\{ \int_{t_0}^{t_0 q^\omega} \frac{e_{-a}(t,\sigma(s))}{\mu(t)^2 g^2(t)} \Delta t + \lambda \int_{\sigma(s)}^{t_0 q^\omega} \frac{e_{-a}(t,\sigma(s))}{\mu(t)^2 g^2(t)} \Delta t \right\} \Delta s, \end{aligned}$$

with equality if K is one-periodic.

Remark 5.2. If we choose $\omega = 1$, i.e., $a(t) = \frac{\alpha}{t}$ and $K(t) = \frac{\kappa}{t}$, for a and K positive constants, the right-hand side of (5.1) is

$$\begin{aligned}
&\lambda \int_{t_0}^{t_0 q} \kappa\alpha \Big\{ \int_{t_0}^{\sigma(s)} \frac{e_{-a}(t,\sigma(s))}{\mu(t)^2 g^2(t)} \Delta t + (\lambda+1) \int_{\sigma(s)}^{t_0 q} \frac{e_{-a}(t,\sigma(s))}{\mu(t)^2 g^2(t)} \Delta t \Big\} \\
&\overset{(2.1)}{=} \lambda\mu(t_0)\kappa\alpha \Big\{ \int_{t_0}^{t_0 q} \frac{e_{-a}(t,qt_0)}{\mu(t)^2 g^2(t)} \Delta t + (\lambda+1) \int_{t_0 q}^{t_0 q} \frac{e_{-a}(t,t_0 q)}{\mu(t)^2 g^2(t)} \Delta t \Big\} \\
&= \lambda\mu(t_0)\kappa\alpha\mu(t_0) \frac{e_{-a}(t_0,t_0 q)}{\mu(t_0)^2 g^2(t_0)} = \lambda\kappa\alpha \frac{e_{-a}(t_0,t_0 q)}{g^2(t_0)} \\
&= \lambda\kappa\alpha \frac{e_{-a}(t_0,t_0 q)}{\left(e_{-a}(t_0,t_0 q) a(t_0) t_0\right)^2} = \lambda\kappa \frac{e_{-a}(t_0,t_0 q)}{\alpha(e_{-a}(t_0,t_0 q))^2} \\
&= \frac{\kappa}{\alpha} \frac{q e_{-a}(t_0,t_0 q) - 1}{e_{-a}(t_0,t_0 q)} = \frac{\kappa}{\alpha}(q-1)(1+\alpha) \overset{(2.2)}{=} \frac{\alpha+1}{\alpha} \int_{t_0}^{t_0 q} K(t)\Delta t,
\end{aligned}$$

which is consistent with (3.7).

We can also relate weighted averages of the periodic solution and periodic carrying capacity.

Theorem 5.3. *The weighted average of the periodic solution is strictly less than a weighted average of the carrying capacity, i.e.,*

$$\frac{1}{\omega(q-1)} \int_{t_0}^{q^\omega t_0} w_1(t)\bar{x}(t)\Delta t < \frac{1}{\omega(q-1)} \int_{t_0}^{q^\omega t_0} w_2(t) K(t)\Delta t, \tag{5.2}$$

where

$$w_1(t) = -qt(-a \ominus P), \qquad w_2(t) = w_1(t)\frac{1+ta(t)}{ta(t)},$$

where $P = \frac{p^\Delta}{p}$*, and* $p(t) = t$*. Equality is obtained if* K *has the same period as* α*, given by* $K(s) = C\frac{a(s)}{1+\mu(s)a(s)}$*, where* C *is any constant.*

Proof. Let us define the following functions to simplify the notation: $m(t) = \frac{1}{\mu(t)ta(t)}$, and $n \oplus m = -a$; so m, n are ω-periodic. Let $\Phi = -a \ominus P$. It is not hard to show that $e_P(t,s) = \frac{t}{s}$, for $\frac{p^\Delta}{p}$, and $p(t) = t$.

We have

$$
\begin{aligned}
\int_{t_0}^{q^\omega t_0} w_1(t)\bar{x}(t)\Delta t &\overset{(3.6)}{=} \int_{t_0}^{q^\omega t_0} w_1(t)\frac{\lambda}{\int_t^{q^\omega t} e_{-a}(t,qs)\frac{a(s)}{K(s)}\Delta s}\Delta t \\
&= \int_{t_0}^{q^\omega t_0} w_1(t)\frac{\lambda}{\int_t^{q^\omega t} e_n(t,qs)e_m(t,qs)\frac{a(s)se_{\ominus m}(s,t)}{K(s)se_{\ominus m}(s,t)}\Delta s}\Delta t \\
&< \lambda\int_{t_0}^{q^\omega t_0} \frac{w_1(t)\int_t^{q^\omega t} e_{n\ominus m}(t,qs)a(s)K(s)s^2e^2_{\ominus m}(s,t)\Delta s}{\left(\int_t^{q^\omega t} e_n(t,qs)a(s)se_{\ominus m}(s,t)\Delta s\right)^2}\Delta t \\
&= \lambda\int_{t_0}^{q^\omega t_0} \frac{w_1(t)\int_t^{q^\omega t} e_{n\oplus m}(t,qs)a(s)K(s)s^2e^2_{m}(qs,s)\Delta s}{\left(\int_t^{q^\omega t} e_{n\oplus m}(t,qs)a(s)se_{m}(qs,s)\Delta s\right)^2}\Delta t \\
&= \lambda\int_{t_0}^{q^\omega t_0} \frac{w_1(t)\int_t^{q^\omega t} e_{-a}(t,qs)a(s)K(s)s^2(1+\mu(s)m(s))^2\Delta s}{\left(\int_t^{q^\omega t} e_{-a}(t,qs)a(s)s(1+\mu(s)m(s))\Delta s\right)^2}\Delta t \\
&= \lambda\int_{t_0}^{q^\omega t_0} \frac{w_1(t)\int_t^{q^\omega t} e_{-a}(t,qs)a(s)K(s)s^2(1+\mu(s)m(s))^2\Delta s}{\left(\int_t^{q^\omega t} e_{-a}(t,qs)e_{\ominus P}(t,qs)\frac{t}{q}a(s)(1+\mu(s)m(s))\Delta s\right)^2}\Delta t \\
&= \lambda\int_{t_0}^{q^\omega t_0} \frac{w_1(t)\int_t^{q^\omega t} e_{-a}(t,qs)a(s)K(s)s^2(1+\mu(s)m(s))^2\Delta s}{\left(\int_t^{q^\omega t} -e_{\Phi}(t,qs)t(-\Phi(s))\Delta s\right)^2}\Delta t,
\end{aligned}
$$

where we have used that

$$
\begin{aligned}
q\Phi(s) = q\left(-a\ominus P\right)(s) &= -a(s) - \frac{p^\Delta(s)}{p(s)} = -a(s) - \frac{1}{\mu(s)}(q-1) \\
&= -a(s) - \frac{1}{s} = -a(s)\left(1+\frac{1}{a(s)s}\right) = -a(s)(1+\mu(s)m(s)).
\end{aligned}
$$

We can further simplify the right hand side, using $w_2(s) := a(s)s(1+\mu(s)m(s))^2$ (therefore w_2K is ω-periodic):

$$\overset{(2.4)}{=} \lambda \int_{t_0}^{q^\omega t_0} \frac{w_1(t)}{t^2} \frac{\int_t^{q^\omega t} e_{-a}(t,qs) s w_2(s) K(s) \Delta s}{(e_\Phi(t,q^\omega t)-1)^2} \Delta t$$

$$\overset{(2.9)}{=} \frac{\lambda}{(e_\Phi(t_0,q^\omega t_0)-1)^2} \int_{t_0}^{q^\omega t_0} \frac{w_1(t)}{t^2} \int_t^{q^\omega t} e_{-a}(t,qs) s w_2(s) K(s) \Delta s \, \Delta t$$

$$\overset{(4.4)}{=} \frac{\lambda}{(e_\Phi(t_0,q^\omega t_0)-1)^2} \left\{ \int_{t_0}^{q^\omega t_0} s w_2(s) K(s) \int_{t_0}^{qs} \frac{w_1(t)}{t^2} e_{-a}(t,qs) \Delta t \, \Delta s \right.$$
$$\left. + \int_{q^\omega t_0}^{q^{2\omega} t_0} s w_2(s) K(s) \int_{q^{1-\omega} s}^{q^\omega t_0} \frac{w_1(t)}{t^2} e_{-a}(t,qs) \Delta t \Delta s \right\}$$

$$= \frac{\lambda}{(e_\Phi(t_0,q^\omega t_0)-1)^2} \left\{ \int_{t_0}^{q^\omega t_0} s w_2(s) K(s) \int_{t_0}^{qs} \frac{w_1(t)}{t^2} e_{-a}(t,qs) \Delta t \Delta s \right.$$
$$\left. + \sum_{i=m+\omega}^{m+2\omega-1} (q-1) q^{2i} w_2(q^i) K(q^i) \sum_{j=i+1-\omega}^{m+\omega-1} (q-1) \frac{w_1(q^j)}{q^j} e_{-a}(q^j, q^{i+1}) \right\}$$

$$= \frac{\lambda}{(e_\Phi(t_0,q^\omega t_0)-1)^2} \left\{ \int_{t_0}^{q^\omega t_0} s w_2(s) K(s) \int_{t_0}^{qs} \frac{w_1(t)}{t^2} e_{-a}(t,qs) \Delta t \Delta s \right.$$
$$\left. + \sum_{i=m}^{m+\omega-1} (q-1) q^{2i+\omega} w_2(q^i) K(q^i) \sum_{j=i+1}^{m+\omega-1} (q-1) \frac{w_1(q^j)}{q^j} e_{-a}(q^j, q^{i+\omega+1}) \right\}$$

$$= \frac{\lambda}{(e_\Phi(t_0,q^\omega t_0)-1)^2} \left\{ \int_{t_0}^{q^\omega t_0} s w_2(s) K(s) \int_{t_0}^{qs} \frac{w_1(t)}{t^2} e_{-a}(t,qs) \Delta t \Delta s \right.$$
$$\left. + \int_{t_0}^{q^\omega t_0} s w_2(s) K(s) q^\omega \int_{qs}^{q^\omega t_0} \frac{w_1(t)}{t^2} e_{-a}(t, q^{\omega+1} s) \right\}$$

$$= \frac{-\lambda}{(e_\Phi(t_0,q^\omega t_0)-1)^2} \left\{ \int_{t_0}^{q^\omega t_0} w_2(s) K(s) \int_{t_0}^{qs} \Phi(t) e_{-a\ominus P}(t,qs) \Delta t \, \Delta s \right.$$
$$\left. + \int_{t_0}^{q^\omega t_0} w_2(s) K(s) \int_{qs}^{q^\omega t_0} \Phi(t) e_{-a\ominus P}(t, q^{\omega+1} s) \Delta t \, \Delta s \right\}$$

$$= -\frac{\lambda}{(e_\Phi(t_0, q^\omega t_0) - 1)^2} \Bigg\{ \int_{t_0}^{q^\omega t_0} w_2(s)K(s)(1 - e_\Phi(t_0, qs))\Delta s$$

$$+ \int_{t_0}^{q^\omega t_0} w_2(s)K(s)(e_\Phi(q^\omega t_0, q^{\omega+1}s) - e_\Phi(qs, q^{\omega+1}s))\Delta s \Bigg\}$$

$$\overset{(2.8)}{\underset{(2.9)}{=}} -\frac{\lambda(1 - e_\Phi(t_0, q^\omega t_0))}{(e_\Phi(t_0, q^\omega t_0) - 1)^2} \int_{t_0}^{q^\omega t_0} w_2(s)K(s)\Delta s = \int_{t_0}^{q^\omega t_0} w_2(s)K(s)\Delta s,$$

where we have used that

$$\lambda = q^\omega e_{-a}(t_0, q^\omega t_0) - 1 = e_\Phi(t_0, q^\omega t_0) - 1.$$

Dividing both sides by $\omega(q - 1)$ yields the result. □

Example 5.4. Consider the case of a one-periodic growth rate, i.e., $a(t) = \alpha/t$, then the previous Theorem reads as

$$\int_{t_0}^{q^\omega t_0} \bar{x}(t)\Delta t < \frac{\alpha + 1}{\alpha} \int_{t_0}^{q^\omega t_0} K(t)\Delta t, \tag{5.3}$$

which is consistent with [5, Theorem 5.6]. To realize it, note that

$$w_1(t) = \alpha + 1, \qquad w_2(t) = \frac{(1 + \alpha)^2}{\alpha},$$

because

$$w_1(t) = -qt\,(-a(t) \ominus P) = -qt\left(-\frac{a(t)}{q} - \frac{(q-1)}{q\mu(t)}\right) = \alpha + 1,$$

and therefore

$$w_2(t) = w_1(t)\frac{1 + ta(t)}{ta(t)} = (\alpha + 1)\frac{1 + \alpha}{\alpha}.$$

This is consistent with (3.7).

REFERENCES

[1] J. Barić, R. Bibi, M. Bohner, A. Nosheen, J. Pečarić, *Jensen Inequalities on Time Scales*, Monographs in Inequalities, vol. 9, Theory and Applications, Element, Zagreb, 2015.

[2] L. Berezansky, E. Braverman, *On impulsive Beverton–Holt difference equations and their applications*, J. Differ. Equations Appl. **10** (2004) 9, 851–868.

[3] R.J.H. Beverton, S.J. Holt *On the dynamics of exploited fish populations*, Fishery Investigations (Great Britain, Ministry of Agriculture, Fisheries, and Food), vol. 19, H. M. Stationery Off., London, 1957.

[4] M. Bohner, R. Chieochan, *Floquet theory for q-difference equations*, Sarajevo J. Math. **8** (2012) 21, 355–366.

[5] M. Bohner, R. Chieochan, *The Beverton–Holt q-difference equation*, J. Biol. Dyn. **7** (2013) 1, 86–95.

[6] M. Bohner, A. Peterson, *Dynamic Equations on Time Scales: An Introduction with Applications*, Birkhäuser Boston, Inc., Boston, MA, 2001.

[7] M. Bohner, A. Peterson, *Advances in dynamic equations on time scales*, Birkhäuser Boston, Inc., Boston, MA, 2003.

[8] M. Bohner, S. Stević, H. Warth, *The Beverton–Holt difference equation*, [in:] Discrete Dynamics and Difference Equations, World Sci. Publ., Hackensack, NJ, 2010, pp. 189–193.

[9] M. Bohner, S.H. Streipert, *The Beverton–Holt equation with periodic growth rate*, Int. J. Math. Comput. **26** (2015) 4, 1–10.

[10] M. Bohner, S.H. Streipert, *The Beverton–Holt q-difference equation with periodic growth rate*, [in:] Difference Equations, Discrete Dynamical Systems, and Applications. Springer-Verlag, Berlin, Heidelberg, New York, 2015, pp. 3–14.

[11] Å. Brännström, D. Sumpter, *The role of competition and clustering in population dynamics*, Proc. R. Soc. B **272** (2005) 1576, 2065–2072.

[12] J.M. Cushing, S.M. Henson, *Global dynamics of some periodically forced, monotone difference equations*, J. Differ. Equations Appl. **7** (2001) 6, 859–872.

[13] T. Diagana, *Almost automorphic solutions to a Beverton–Holt dynamic equation with survival rate*, Appl. Math. Lett. **36** (2014), 19–24.

[14] S.A. Geritz, É. Kisdi, *On the mechanistic underpinning of discrete-time population models with complex dynamics*, J. Theor. Biol. **228** (2004) 2, 261–269.

[15] M. Holden, *Beverton and Holt revisited*, Fisheries Research **24** (1995) 1, 3–8.

[16] T. Radulescu, V. Radulescu, T. Andreescu, *Problems in Real Analysis: Advanced Calculus on the Real Axis*, Springer, 2009.

[17] O. Tahvonen, *Optimal harvesting of age-structured fish populations*, Mar. Resour. Econ. **24** (2009) 2, 147–169.

[18] F.-H. Wong, C.-C. Yeh, W.-C. Lian, *An extension of Jensen's inequality on time scales*, Adv. Dyn. Syst. Appl. **1** (2006) 1, 113–120.

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